

## Mating Status and Choice of Group Size in the Phoretic Fly *Norrbonomia frigipennis* (Spuler) (Diptera: Sphaeroceridae)

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Accepted September 12, 2002; revised March 18, 2003

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*The phoretic sphaerocerid fly Norrbombia frigipennis mates on scarabid dung beetles, follows them underground, and lays eggs in the collected dung. We found that male and female flies distribute themselves nonrandomly on beetles with respect to fly group size. The proportion of virgin females increased with group size, and females with mature eggs were most frequently found on beetles carrying fewer flies. Laboratory experiments revealed that mated females avoided larger groups, virgin females seemed to prefer large groups and mated females, small groups. Males showed no such pattern. These results suggest that N. frigipennis can estimate group size, presumably an adaptation with a reproductive function. However, flies did not join hosts on the basis of the sex of already mounted flies.*

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**KEY WORDS:** Sphaeroceridae; *Norrbonomia frigipennis*; group size; dung beetles.

### INTRODUCTION

Many animals spend part or most of their lives in groups (Alcock, 1993). These groups may be the result of individuals attracted to a specific resource or habitat and/or attraction to conspecifics. One common purpose for aggregation is mating, although this may be combined with other behaviors,

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such as searching for food and oviposition sites. Within aggregations the competition among individuals of the same sex for breeding resources may be intense. Moreover, males and females compete over different resources. For example, males may compete for access to females, whereas females may compete for oviposition sites. Therefore the nature and intensity of intrasexual competition may differ between the sexes (cf. Trivers, 1972; Low, 1978; Alexander and Borgia, 1979), and "optimal" group sizes for males and females may be different.

A number of tiny flies have intimate relationships with larger arthropods. Some are phoretic, that is, they spend considerable amount of time on their "host," not feeding on the larger animal but simply waiting for it to perform some useful function (cf. Sivinski *et al.*, 1999). In the southeastern United States four species of Sphaeroceridae, including *Norrbomia frigipennis* (Spuler), are phoretic kleptoparasites. Females oviposit in the buried dung caches of scarab beetles (see Sivinski, 1983). These beetles often gather at high densities at animal droppings, thereby providing flies with opportunities for host choice. Female flies reach subterranean oviposition sites by riding on beetles near dung and following their host underground (Sivinski, 1983). Males apparently ride to encounter females (Sivinski, 1984; cf. Zeh and Zeh, 1992a,b). Flies are frequently observed mating while riding on beetles and females spend up to 70% of their riding time in repeated copulations with a variety of males (Sivinski, 1983). Males also accompany beetles underground and males probably submit to internment to win sperm competitions. In many insect species, the last male to mate fathers the majority of offspring (Parker, 1970; Walker, 1980), although the generality of this conclusion has been strongly challenged (Simmons and Siva-Jothy, 1998). Since oviposition occurs underground, opportunities for males to obtain last copulations will also be subterranean. Alternatively, males may gain by mating with the female repeatedly, as this might also increase paternity.

For *N. frigipennis*, the potential mounts (beetles) are ambulatory islands whose surfaces bear a variety of reproductive environments. The "hosts" will generally carry different numbers and "qualities" (such as mating status or fighting ability) of potential mates and competitors. When comparison of mounts is possible, sexual opportunity might influence host selection. Evidence of choices being made on the basis of mate seeking and the avoidance/displacement of rivals can be found in deviations from random distributions of phoretics upon their hosts. For example, males might prefer larger groups because the opportunity to encounter receptive females might increase with group size. However, because riding males fight, subordinate males might be forced to seek receptive females in smaller groups or to occupy an empty beetle and wait for females. Mated females might avoid large groups for two reasons. First, by riding on beetles with no or few mounts they might

reduce harassment from courting males. Second, the fewer females riding on a beetle, the fewer females will use the buried dung for egg laying. Virgin females might join large groups because the probability of finding a good mate may be higher there than in smaller groups.

This study has two aims. First, to investigate whether males and females of *N. frigipennis* distribute themselves nonrandomly with respect to group size on the beetles. Second, if such a pattern exists, can it be explained by differences in the behavior of mated and virgin males and females.

## MATERIALS AND METHODS

### Field Samplings

In the field, a circle with a radius of 1 m was drawn around an artificially placed pile of pig dung (6–12 h old). Beetles, predominantly the common “ball-rolling” species *Canthon pilularius* (L.), leaving the mass with flies on board were collected as they crossed the 1-m line. A vial was placed in front of the beetle, which crawled into it without disturbing the phoretic flies. The summed sex ratio data were taken during 3 different years. J.S. made collections in 1980 and 1981 (313 beetles, 3707 flies) in Alachua County, Florida, and E.P. collected 100 beetles (1184 flies) in 1993 in cattle pastures near Newberry, Alachua County, Florida, and Shell Mound State Preserve, Levy County, Florida. In all 3 years collections were made in from May to July, flies were collected until about half of the dung had been “consumed,” which takes about 1.5 h.

Seventy-seven of the beetles collected 7 May–12 July 1993 were frozen on dry ice to prevent the phoretic flies from further mating. The female flies were dissected to establish degree of egg maturity and presence of sperm in spermathecae. Egg maturity was measured as follows: 1 = unyolked; 2 = yolking; 3 = color developing, fully yolked; 4 = mature. Previous dissections of laboratory-reared females revealed that females do not emerge with fully matured eggs. Egg maturity was based on the most mature egg in each female, and there were typically several eggs (5–15) at about the same stage of maturation. All females, even those having mature eggs, had at least five unyolked eggs.

### Laboratory Experiments

Throughout the laboratory experiments only laboratory-reared flies were used. The flies had no experience of beetles and were 3–5 days old. The fly larvae were reared in a mixture of cow manure, dried, grounded corn,

wheat flour, and water. When the larvae had pupated, they were carefully removed from the dung mixture and placed individually in small gelatin capsules. In total 5813 pupae were removed from the dung and 33.5% (1945) of these emerged. The sex ratio of the newly emerged flies was 847 males:1098 females (i.e., proportion males = 0.435 [cf. Sivinski, 1983]). After eclosion the flies were sexed and put in 0.5-L glass milk bottles (45–50 flies in each bottle) with ca. 0.1 L of the dung mixture at the bottom. The sexes were either kept separately or mixed to achieve mated individuals. In total 1280 flies were used in the experiment.

In order to investigate how different categories of flies chose among different group sizes of flies on a beetle, a pair of dead beetles (hornless *Phaneus ignius* MacLeay) was presented to a batch of 40 flies consisting of either virgin males, mated males, virgin females, or mated females. The beetles were glued on a transparent plastic sheet (circular; diameter, 60 mm) to which a string was fastened. Each pair consisted of one beetle with freeze-dried *N. frigipennis* flies glued on the thorax and one empty beetle (some glue was smeared on the thorax). Three different group sizes of freeze-dried flies were used, 3, 5, and 10 flies, one setup for each sex of flies. Thus, each batch of flies was presented to six pairs of beetles, in a randomized sequence. Freeze-dried flies that came loose and fell off were replaced by new ones and the position of the beetles was alternated between replicates. The beetles were pulled by hand on a layer of sand in a plastic transparent cylinder (cf. Petersson and Sivinski, 1996). Beetles were pulled back and forth four times during each presentation at a standard speed. We noted the number of flies that landed on each beetle or just followed the beetles. The proportion of flies following ( $0.145 \pm 0.079$ ) was about three times higher than the proportion landing ( $0.049 \pm 0.015$ ). Because the following flies could not be unambiguously assigned to a single beetle, the following flies were excluded in the analyses. Individual flies could not be traced, for obvious reasons, and therefore some flies might have hopped on and off the beetles, resulting in the possibility that some flies were counted several times. However, of 20 trials with a single fly, only 2 flies (a mated male and a virgin female) visited the beetles twice, 14 flies made a single visit, and 4 did not visit at all. This gives an average visiting rate of 1.125 (nonvisiting flies excluded). This experiment was carried out indoors, and a total of 32 trials was made (i.e., six pairs of beetles were presented to eight different batches of each category of flies).

### Statistical Treatments

For the laboratory data the proportion of flies mounting was calculated and arcsin-transformed. First, the effects of glued fly sex and group size were

analyzed. When no effects could be detected the data for both sexes were pooled. The mean proportions of mounting for each batch and group size were calculated, which resulted in a sample size of 128. As this sample size is larger than the actual one (32), the probability values have been corrected using the Šidák (1967) method. The laboratory data were analyzed by use of a four-way ANOVA and, when appropriate, further analyzed with pairwise *t*-tests on least-square means. For the field sampling nonparametric analysis was performed for data concerning egg maturity and the fly distribution on beetles, due to ordinal level of measurement and to nonnormal distribution, respectively. All statistical analyses were made using SAS statistical software (SAS Institute, 1987) and all tests are two-tailed. Data are presented as mean  $\pm$  one standard error of mean.

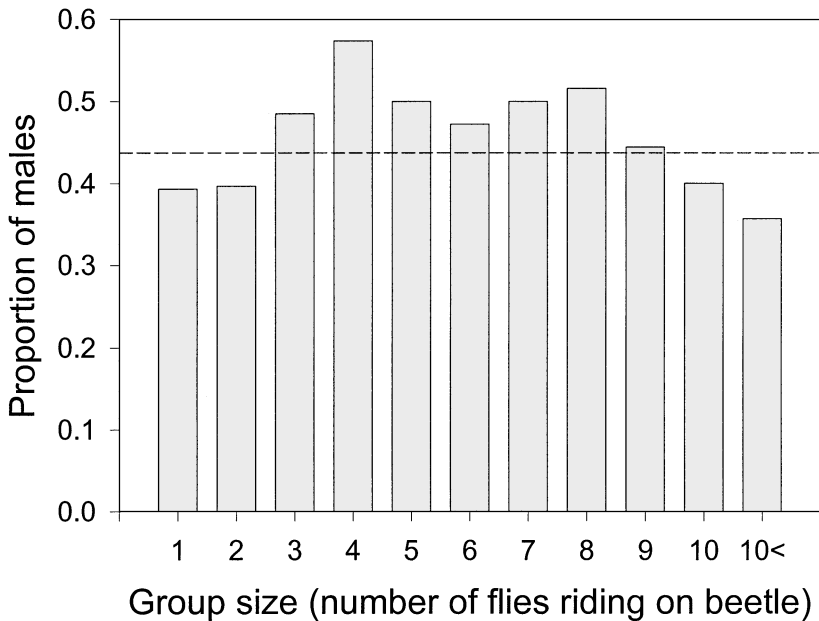
## RESULTS

### Distribution of Flies on Beetles

*Field Samples.* There were no differences in fly sex ratio among the samples from the various years. Proportion of males on walking scarabs was 0.48 in 1980–1981 (cf. Sivinski, 1983) and 0.45 in 1993 ( $\chi^2 = 3.28$ ,  $P = 0.0701$ ). The relative abundance of *N. frigipennis* and beetles was approximately consistent over the time sampled; that is, beetles and flies arrived at dung at similar rates, so that the mean number of flies per beetle does not rise or fall significantly over the time the sample was taken. None of the samples had significant correlations between the order of beetles crossing the 1-m line and the number of flies carried (1980–1981,  $r_s = 0.058$ ,  $P = 0.68$ ; 1993,  $r_s = 0.047$ ,  $P = 0.77$ ; Spearman rank correlation).

The rise and fall in mean group sex ratio as group size increases are shown in Fig. 1 ( $\chi^2 = 25.57$ ,  $P < 0.004$ ). Both females and males were nonrandomly distributed among beetles. Females were overrepresented in both small groups and larger groups, and males in medium-sized groups. Riderless beetles were underrepresented in the field samples, and both fly sexes seemed to prefer aggregations. The distribution of the sexes differed significantly ( $\chi^2 = 36.92$ ,  $df = 2$ ,  $P < 0.001$ ; Kolmogorov–Smirnov two-sample test). Females seemed to have a lower degree of avoidance of small groups, compared to males, and a higher preference for larger groups.

*Laboratory Experiments.* There was no observed effect due to the sexual composition of the fly groups (sex of glued flies,  $F_{1,192} = 4.02$ ,  $P = 0.188$ ; group size,  $F_{2,192} = 5.82$ ,  $P = 0.053$ ; interaction terms,  $F_{2,192} = 2.30$ ,  $P = 0.376$ ). The pulling speed of the dead beetles had no effect on the number flies landing on the beetles ( $r = -0.055$ ,  $P = 0.185$ ; product-moment



**Fig. 1.** Mean proportions of males in different-sized groups of the sphaerocerid fly *Norrbomia frigipennis* riding on scarab beetles. The dashed line represents the average proportion of males (0.437) in the samples taken in the field (cf. Sivinski, 1983). The distribution differs from random ( $\chi^2 = 25.57$ ,  $P < 0.004$ ). Sample sizes are as follows (group size: No. of beetles): 1:173, 2:87, 3:33, 4:34, 5:18, 6:12, 7:8, 8:8, 9:3, 10:5,  $\geq 11$ :22.

correlation, pooled with fly category and group size of freeze-dried flies on beetles). On average, males and females were equally attracted to the beetles (proportion landed: females,  $0.044 \pm 0.0024$ ; males,  $0.047 \pm 0.0025$ ,  $t = 0.89$ ,  $P = 0.973$ ; cf. Table I).

### Differences Between Virgin and Mated Flies

*Field Samples.* The sex of the *N. frigipennis* that joined a particular group size can be determined by the changes in the sex ratios from one group size to the next. Observed and expected distributions in group sizes with reasonably large membership are listed in Table II. No significant deviations from random could be found, i.e., flies did not join groups on the basis of cooccupant sex.

In total, 164 females were collected in the field and later dissected. Of these, 14 (8.5%) were found to be uninseminated. The proportion of

**Table I.** The Outcome of Three-Way ANOVA on Laboratory Data Concerning the Proportions of Flies Landing on Either an Empty Dead Beetle or a Dead Beetle with Freeze-Dried Flies Glued on It<sup>a</sup>

Source	df	F value	P value
Sex	1	1.47	0.644
Mating status	1	34.48	0.001
Group size	3	4.31	0.025
Sex * mating status	1	0.49	0.931
Sex * group size	3	6.01	0.004
Sex * mating status * group size	3	2.17	0.331

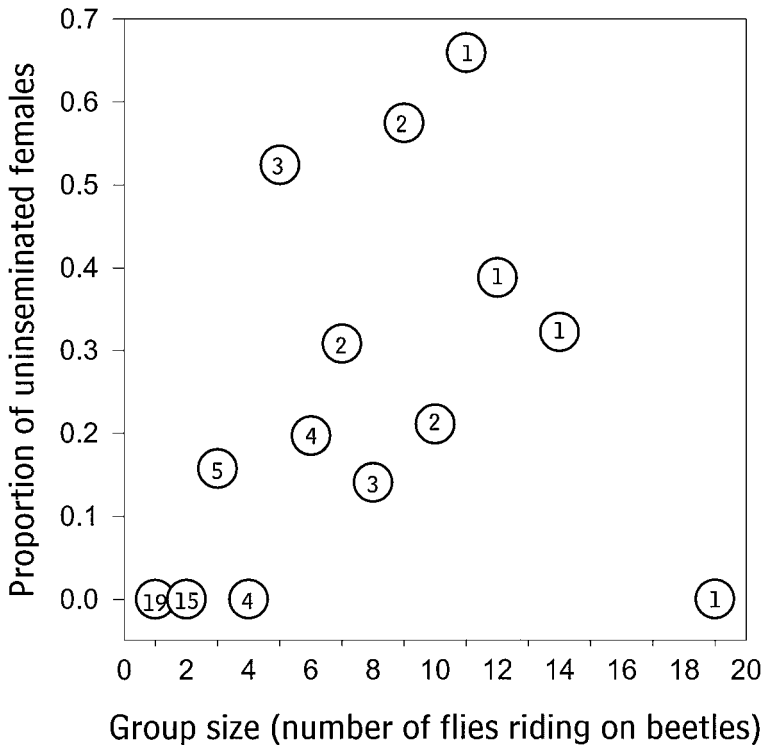
<sup>a</sup>Sex refers to the gender of the living flies; mating status to whether or not the flies were virgins; and group size to the number of freeze-dried flies glued on the beetles. The probability values have been corrected for multiple comparisons (see text for more details).

uninseminated females increased with group size ( $r^2 = 0.363$ ,  $F = 6.86$ ,  $P < 0.023$ ; data weighted for number of beetles) (Fig. 2). There was no correlation between the proportion of males and the proportion of virgin females ( $r^2 = 0.147$ ,  $F = 2.064$ ,  $P = 0.176$ ). The egg-maturity index of the dissected females decreased with group size, that is, females with mature eggs were most frequently found on beetles with fewer flies riding on them (Fig. 3).

*Laboratory Experiments.* Virgin individuals were more attracted to beetles than mated individuals (virgins,  $0.053 \pm 0.0026$ ; mated,  $0.028 \pm 0.0023$ ;  $t = 2.75$ ,  $P = 0.039$ ). Flies landed more frequently on the occupied beetle

**Table II.** The Numbers of Beetles Observed and Expected to Carry the Various Possible Gender Assortments of *Norrbomia frigipennis* in Groups of from Two to Five Flies (No. Males:No. Females)

						<i>n</i>	$\chi^2$
Group size, 2	2:0	1:1	0:2				
Observed	12	45	38			95	0.06 (n.s.)
Expected	12.53	43.94	38.53				
Group Size, 3	3:0	2:1	1:2	0:3			
Observed	2	15	15	4		36	1.62 (n.s.)
Expected	3.79	12.71	14.21	5.29			
Group size, 4	4:0	3:1	2:2	1:3	0:4		
Observed	3	11	15	6	1	36	0.97 (n.s.)
Expected	2.91	10.19	13.38	7.81	1.71		
Group size, 5	5:0	4:1	3:2	2:3	1:4	0:5	
Observed	0	3	7	6	3	0	19 1.37 (n.s.)
Expected	0.63	3.06	5.99	5.87	2.88	0.56	



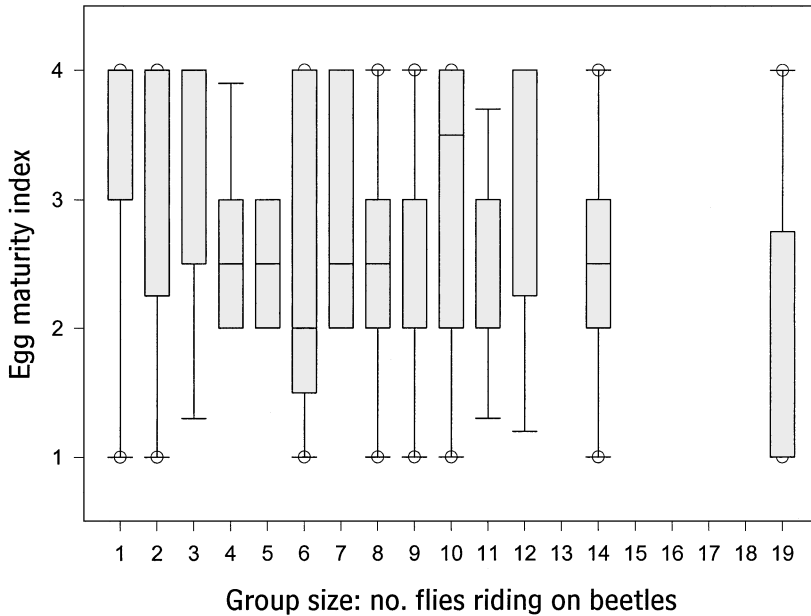
**Fig. 2.** Mean proportions of virgin females in different-sized groups of the sphaerocerid fly *Norrbonnia frigipennis* riding on scarab beetles. The proportion of virgin females increases with group size (proportion virgin females [arsin-transformed] =  $-0.001 + 0.0286 * \text{group size}$ ;  $F = 6.86$ ,  $r^2 = 0.363$ ,  $P < 0.023$ ); the regression was weighted for number of beetles. The numbers denote sample sizes (number of beetles).

( $0.053 \pm 0.0027$ ) than on the riderless alternative ( $0.038 \pm 0.0021$ ;  $t = 4.56$ ,  $P < 0.001$ ). One interaction term was found to be significant, sex  $\times$  group size (Table I). This indicates that males and females responded differently to the group sizes on beetles. Most categories tended to have a preference for beetles already occupied (cf. Fig. 4). However, mated females avoided the largest group presented to them (Fig. 4).

## DISCUSSION

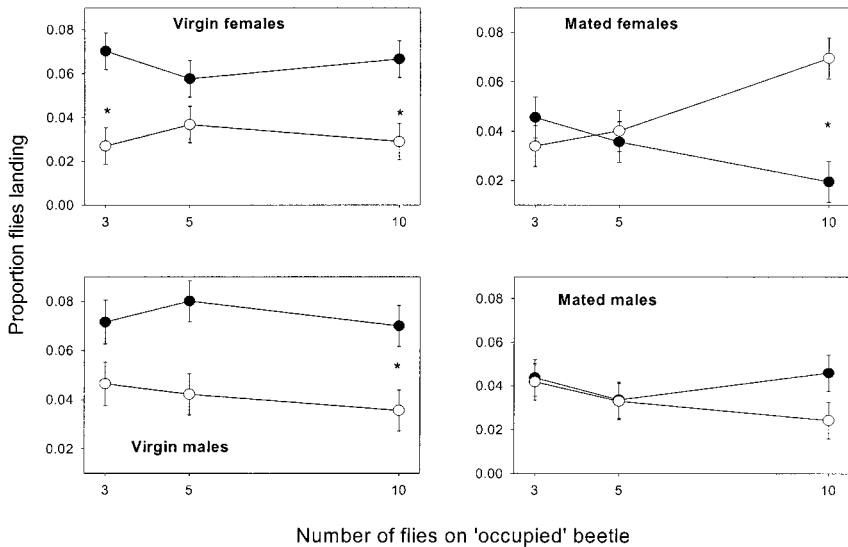
This study clearly shows that the sexes of *N. frigipennis* respond differently to various beetle back fly densities. The actual group size distribution





**Fig. 3.** Egg-maturity index of females in different-sized groups of the sphaerocerid fly *Norrbomia frigipennis* riding on scarab beetles. A higher value of egg-maturity index represents more mature eggs (4 means that the most mature egg of a female was fully matured). Median egg-maturity index decreases with group size ( $r_s = -0.584$ ,  $P < 0.05$ ). Sample sizes as in Fig. 2.

shapes are complex. First, beetles are mounted if other flies are present; empty beetles were far less frequent than expected from random mounting. Second, it appears that virgins of both sexes preferred the more crowded beetles. The data for smaller groups are more equivocal, but mated females seemed to have a higher preference than males for smaller groups. Thus, the distribution pattern found in field samples (Fig. 1) was due mostly to mated female preference for small groups and virgin females preference for large groups. The frequency of virgin females increased with group size, which suggests that these females preferred large groups, presumably because the probability of encountering high-quality males increased with group size. In addition the egg-maturity index decreased with increasing group size and many mated females did not contain fully mature eggs. This suggests that females remate and that some of the females attracted to large groups might be mated females that have laid eggs and are seeking to be reinseminated. Mated females that were ready to lay eggs might benefit from joining small groups or mounting empty beetles. The harassment from courting males could be reduced by such behavior, as well as competition among larvae



**Fig. 4.** Mean proportions of four categories of *Norrbomia frigipennis* landing on either an empty dead beetle (open circles) or a dead beetle with freeze-dried flies glued on it (filled circles; see text for more details). The error bars denote one standard error of the mean. "Beetle-pairs" where the proportions of flies landing differed significantly (at the 0.05 level) between the occupied and the empty beetle are marked with an asterisk.

from different broods. In several insect species life span is inversely related to the rate of energy expenditure and injuries incurred during copulation (e.g., White and Bell, 1993). The difference between mated and virgin females was confirmed by the laboratory experiment, mated females avoided large aggregations and preferred empty beetles. Mated males, on the other hand, did not show any specific preference for any group size.

Alternatively, the distribution of female *N. frigipennis* in the field could be explained by some hosts being especially attractive, for fly-independent reasons. If so, unusually large numbers of flies might accumulate on such scarabs. There is, however, no consistent pattern of support for this argument. Correlations between host quality (large dung cache, small host size, i.e., small host appetite) and number of flies borne were generally insignificant (Sivinski, 1983). Petersson and Sivinski (1996) found that flies are slightly more attracted to larger beetles, but this pattern occurred only with *Phanaceus* species. With *C. pilularius*, which made up 98% of the beetles included in this study, no such pattern was found.

As flies became more abundant relative to hosts, females tended to be more clumped (i.e., had higher variance relative to the mean) in their distribution ( $r = -0.45$ ,  $n = 15$ ,  $P < 0.05$ ). One interpretation of this correlation

is that, the higher the fly density, the more likely it is that large clumps will initially be formed by chance and so females are more likely to encounter and respond to attractively sized groups at high densities. Interestingly, phoretic mites, which apparently do not mate on hosts, become more uniformly distributed at high densities, perhaps because of competitor avoidance (Binns, 1974).

The changing distribution of the sexes over group size shows that *N. frigipennis* can estimate the abundance of conspecifics, presumably an adaptation with a reproductive function. It also shows that group size influenced the choice of resource, i.e., which beetle to ride. There is, however, no evidence that flies joined hosts on the basis of the gender of already mounted flies. If large group-joining females were searching for mates, they did so on the basis of probability rather than the certain "knowledge" of male presence; there is almost no sexual dimorphism, and recall the essentially random frequencies of possible gender combinations (Table I). Inability to recognize gender without intimate, sometimes prolonged, contact is a puzzling but commonplace event among Diptera (see Borgia [1979] for a discussion), and other insects groups as well (see, e.g., White and Bell, 1993). In the laboratory experiment there were no differences in the attractiveness of male and female groups. As these groups consisted of freeze-dried flies, there was no possibility of pheromonal communication that could allow gender determination. However, the field data revealed that there was no change in the sex ratio from one group size to the next (Table I), i.e., flies did not join groups on the basis of cooccupant gender.

Insect males often obtain sexual opportunities by occupying valuable resources (e.g., Thornhill and Alcock, 1983). This study shows that insect females may also choose a particular resource because of its sexual opportunities. In the yellow dungfly *Scatophaga stercoraria* females did not appear to choose dung masses on the basis of the males that occupied them. The differences in female behavior in the two species may be due to differences in group size. When the number of males is relatively large at a resource (*S. stercoraria*), all resources may contain a sample of relatively fit males with which to mate (cf. Borgia, 1979). When the average number of males is low (i.e., *N. frigipennis*), then it may be best to discriminate among groups of conspecifics riding on beetles and choose those most likely to provide the best sexual opportunity.

#### ACKNOWLEDGMENTS

We thank Jim Nation, Kevina Vulinec, and two anonymous reviewers for valuable criticism and comments on various versions of the manuscript.

The farmer's at Newberry that permitted us to do the field experiments on their cattle fields are very much appreciated. Paul Skelly kindly made the critical-point drying of fly specimens. Most of this study was completed during E. Petersson's postdoctoral stay at USDA in Gainesville, Florida, on the courtesy of the Research Council of Natural Sciences, Sweden.

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